

ABUNDANCE AND DISTRIBUTION OF THE LARVAE OF THE PINK SHRIMP (*PENAEUS DUORARUM*) ON THE TORTUGAS SHELF OF FLORIDA, AUGUST 1962–OCTOBER 1964^{1,2}

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ABSTRACT

A 2-year study has shown that an estimated 870×10^{10} first protozoae of pink shrimp are produced each year within the main part of the Tortugas spawning grounds. Survival rates are nearly constant and average 80.4 percent per day throughout larval life. Estimates of larval survival at specific sampling stations are influenced by the migration patterns of the larvae and vary considerably, depending on whether the sampling station receives older larvae from adjacent areas or loses larvae to other areas.

An investigation of bottom currents on the Tortugas grounds has shown that the prevailing westerly and

southwesterly currents may carry the larvae into the Florida Current, which, in turn, may transport the larvae to the nursery grounds in the Everglades National Park.

Spawning, measured by the relative abundance of first protozoae, is influenced by moon phase; most spawning occurs during the last half of the lunar month. Spawning activity reaches a maximum when bottom water temperatures are highest; the center of spawning shifts from shallow water into deeper water as the spawning season progresses.

PROCEDURES

The methods we have used covered four activities: selection of study stations, sampling procedures, laboratory techniques, and computer conversion of data.

STUDY AREA

We sampled on a grid system that covered the Tortugas Shelf area (fig. 1); stations were 18.5 km. apart. Ten stations were selected for regular sampling in the area considered by Jones et al. (footnote 6) to be the center of spawning. The stations are designated 50.100, 50.90, 50.80, 50.70, 40.90, 40.80, 40.70, 40.60, 32.70, and 30.58 and were located over depths between 10 and 36 m. (5.5 and 20.0 fathoms). (The latter two stations

The early life history of the pink shrimp, *Penaeus duorarum* Burkenroad, has received considerable attention in recent years. Dobkin (1961) described the early larval stages of *P. duorarum* hatched from eggs spawned in the laboratory, and Ewald (1965) succeeded in rearing all stages in the laboratory. These studies have provided evidence upon which identifications of the larvae in the plankton can be based. Eldred, Williams, Martin, and Joyce (1965) studied the inshore and offshore distribution and abundance of larval and postlarval *P. duorarum* in the Tampa Bay area. Jones, Dimitriou, Ewald, and Tweedy (unpublished manuscript)⁶ described the distribution of pink shrimp larvae over a wide area of the Tortugas Shelf of Florida and located the main spawning grounds.

The purposes of the study reported here were to (1) define quantitatively the seasonal abundance of the planktonic shrimp larvae in the main spawning area on the Tortugas Shelf; (2) investigate the relation between spawning intensity and environmental factors; (3) estimate the mortality rates of various larval stages; and (4) describe how immigration and emigration of larvae affect mortality estimates pertaining to specific sampling stations.

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⁶ "Distribution of early developmental stages of pink shrimp, *Penaeus duorarum*, in Florida waters," by A. C. Jones, D. Dimitriou, J. J. Ewald, and J. Tweedy, Institute of Marine Sciences, University of Miami, for Bureau of Commercial Fisheries Biological Laboratory, Galveston, Tex., 54 MS. pp., 13 figs.

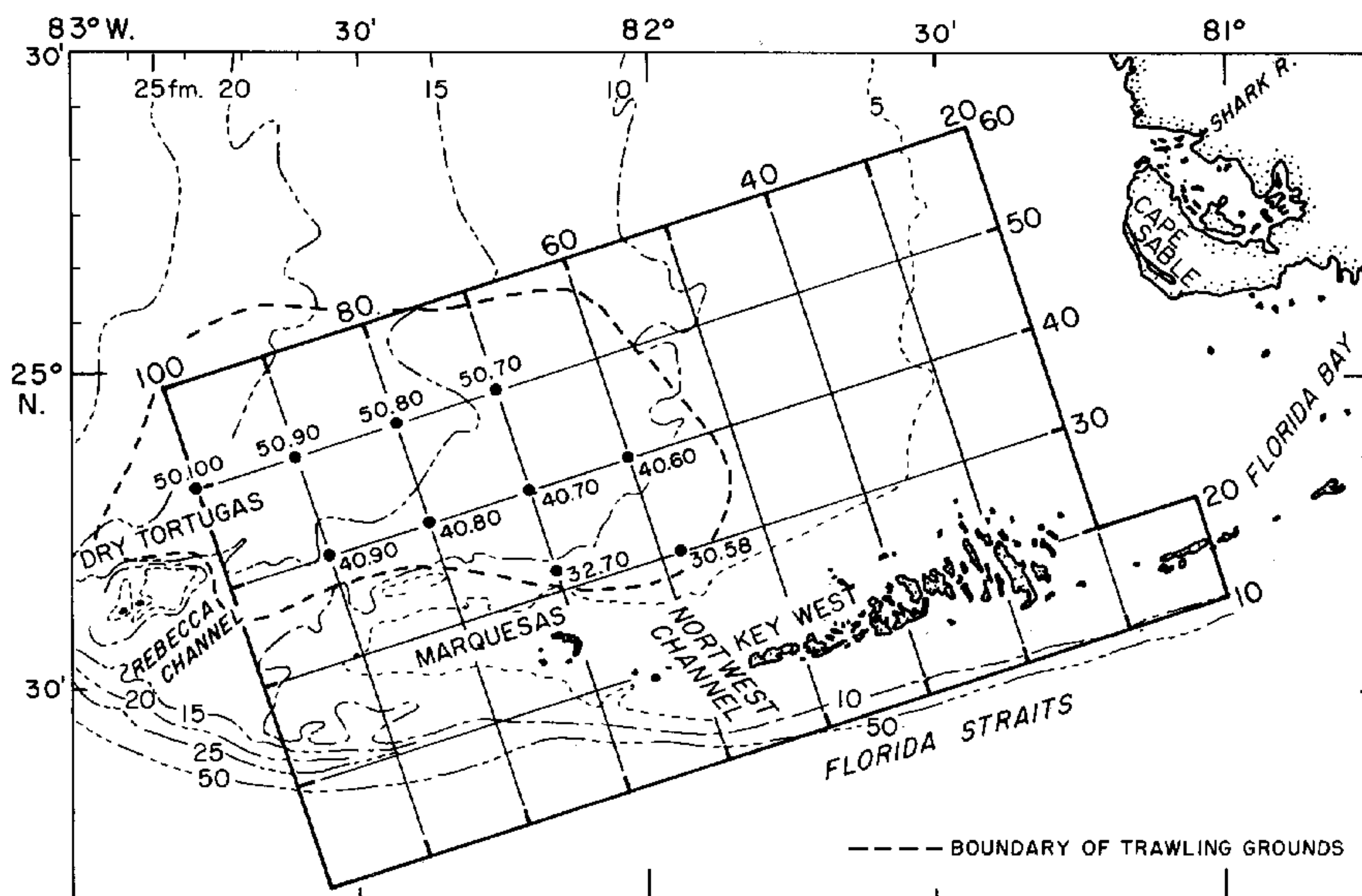


FIGURE 1.—Map of the Tortugas Shelf area showing the sampling grid, regular sampling stations, and place names mentioned in the text.

were slightly displaced from their theoretical grid coordinates because of shoal waters.)

SAMPLING

Throughout the study, we sampled about twice each month. A shrimp trawler 20 m. long overall, having an idling speed of 5.6 km. per hour (3 knots), towed the sampling apparatus. Towing speed varied according to wind velocity and at times was as low as 2.8 km. per hour (1.5 knots).

Gulf V plankton nets were used throughout the study. This net has been described by Arnold (1959) and consists of a metal frame in which is mounted a monel mesh net fitted with a brass bucket in which the plankters accumulate. The mouth diameter of the Gulf V net is 40 cm., and overall length is 100 cm. The mesh has an aperture size of 0.292 mm. Dobkin (1961) stated that first protozoae have a maximum width of 0.35 to 0.44 mm., and all subsequent larval stages are of greater size. Naupliar stages are considerably smaller (maximum width of the fifth nauplius stage is 0.17 to 0.22 mm.) and were not retained by the mesh.

Flowmeters were mounted in the mouths of the nets. These meters were calibrated regularly and

performed consistently over the entire period of operation.

Sampling procedures were rigidly controlled, and, in the event of gear failure or malfunction of timing equipment, the sample was discarded, and the tow was repeated. Replicate samples were taken at each station.

Step-oblique tows were made with the net towed for 3 minutes at each of 10 levels equally spaced between the bottom and surface. When the net was retrieved, the flowmeter reading was noted, and the bucket of plankton emptied. The net was then hosed down thoroughly, and the additional washings were added to the sample. Washing continued until no more plankton or debris appeared in the bucket. Samples were preserved with a 3-percent solution of buffered Formalin.⁷ During the cruise of October 2-6, 1964, when 41 stations were occupied, each level was sampled for 1.5 minutes and tows were reduced to 15 minutes.

Water temperatures were recorded at each station. Surface temperatures were measured with a bucket thermometer, and a trace of the vertical

⁷ Trade names referred to in this publication do not imply endorsement of commercial products.

temperature profile was obtained with a bathythermograph. Samples of the bottom waters were obtained with a Nansen bottle; the salinity of surface and bottom waters was determined on a conductivity bridge in the laboratory. Meteorological observations were recorded in World Meteorological Organization codes.

LABORATORY TECHNIQUES

Plankton sorting was carried out under wide-field, stereoscopic microscopes fitted with variable magnification.

All penaeid shrimp larvae were removed from the samples and identified to genus by using keys developed from descriptions by Pearson (1939), Gurney (1942, 1943), and Heldt (1938). Identification of different stages of *Penaeus* larvae was based on the work of Dobkin (1961). *P. duorarum* is the only member of this genus reported in the Tortugas area (Eldred, 1959); we found no larvae of other species of this genus.

Stages of other penaeid larvae also were identified. Genera encountered included *Trachypeneus*, *Sicyonia*, *Parapenaeus*, and *Penaeopsis*, as well as three unidentifiable species. Several species of *Trachypeneus* and *Sicyonia* occur in the Tortugas area (Eldred, 1959), but the specific identity of these larvae was not determined.

One-half of one of the two samples from each station was usually sorted. The second sample was retained for counting if ambiguities in the flow-meter readings or other data should be encountered. Samples were divided into equal parts by means of a two-compartment, rotating Plexiglas cylinder similar to that designed by Folsom (McEwan, Johnson, and Folsom, 1954).

COMPUTER CONVERSION OF DATA

On the basis of the methods of Ahlstrom (1954) and Sette and Ahlstrom (1948), we designed our data analysis to produce estimates of the abundance of *P. duorarum* larvae and to put the information in a form that could be reproduced easily. The plankton analyses were punched on computer data cards and processed at the Institute of Marine Sciences.

The original counts of the number of larvae in each stage were transformed in two ways. In the first, the numbers of each stage were divided by the volume of water filtered through the Gulf V sampler, giving an estimate of the number of

larvae per cubic meter of water. In the second calculation the numbers of each stage under 10 m.² surface area were estimated by multiplying 10 times the number per cubic meter by the depth of water (in meters) at the station. Unless otherwise specified, values in this report are based upon the numbers of each stage under 10 m.² surface area. All physical and biological data gathered during this investigation were published by Munro and Dimitriou (1967).

VARIABILITY OF ESTIMATES OF LARVAL ABUNDANCE

Reproducibility of plankton hauls and confidence limits to be applied to plankton estimates based upon counts of one-half of a single sample were computed. For estimating this variability, we counted the protozoae in 47 pairs of replicate samples. After reference to the records of flow-meter volume and water depth, counts were adjusted to give estimates of numbers of protozoae present under 10 m.² of surface area (table 1).

Following the methods of Winsor and Clarke (1940) and Silliman (1946), we carried out an analysis of variance to determine the variability of these estimates. Data were subjected to a logarithmic transformation, resulting in a moderately skewed normal distribution. The results of the single-classification analysis of variance are given in table 2.

The mean square between replicate estimates is $0.07319 = \sigma E^2$. The standard deviation of a single estimate (σE) is $\sqrt{0.07319}$, or 0.27054 (a logarithmic value). The 95-percent confidence limits are the antilog of the $2\sigma_E$ value, viz, $2 \times 0.27054 = 0.54108$, and the antilog is 3.476. Percentage confidence limits for the estimates are $1/3.476 \times 100$ and 3.476×100 , or 28.8 and 347.6 percent.

These confidence limits are wider than those obtained by Silliman (1946) and Strasburg (1960), who found that plankton counts at the 95-percent level should be considered significantly different if they were less than half or more than double the sample compared. In the present study, the "half-or-double" rule applies only at the 70-percent level of confidence.

The confidence limits dealt with here, however, include a greater number of sources of variation and error than those of the above-mentioned authors, because the present data were computed numbers of larvae under 10 m.² surface area; thus,

TABLE 1.—Replicate tow data for analysis of variance of catches of *Penaeus duorarum* protozoae, Tortugas Shelf, Florida, August 1962 to October 1964

Tow number	Station number	Month	Year	<i>P. duorarum</i> protozoae	
				Sample 1	Sample 2
				Number per 10 m. ²	
3091-92	40.80	9	1962	461	437
3108-09	40.70	9	1962	1,086	2,102
3110-11	40.70	9	1962	525	823
3112-13	40.70	9	1962	564	766
3116-17	40.70	9	1962	458	708
3124-25	40.80	10	1962	134	180
3209-10	40.60	3	1963	144	290
3211-12	40.70	3	1963	137	130
3213-14	40.80	3	1963	40	9
3233-34	40.80	3	1963	31	30
3306-07	50.70	5	1963	39	39
3348-49	40.70	6	1963	90	124
3381-82	40.60	7	1963	178	195
3383-84	40.70	7	1963	663	370
3385-86	40.80	7	1963	526	382
3387-88	40.90	7	1963	757	962
3389-90	51.00	7	1963	270	192
3391-92	50.90	7	1963	147	167
3395-96	50.70	7	1963	952	742
3401-02	40.60	7	1963	509	200
3405-06	40.80	7	1963	332	362
3419-20	40.70	8	1963	113	11
3421-22	40.70	8	1963	22	99
3425-26	40.70	8	1963	740	267
3427-28	40.70	8	1963	779	299
3393-94	50.80	7	1963	862	647
3432-33	40.60	8	1963	36	94
3434-35	40.70	8	1963	177	48
3446-47	50.70	8	1963	539	200
3452-53	40.60	8	1963	58	215
3466-67	50.70	8	1963	248	143
3520-21	51.00	10	1963	16	140
3638-39	51.00	4	1964	401	459
3640-41	50.90	4	1964	204	340
3642-43	50.80	4	1964	537	707
3652-53	40.70	4	1964	761	433
3694-95	40.80	5	1964	48	163
3811-12	40.80	8	1964	75	81
3813-14	40.80	8	1964	102	264
3815-16	40.80	8	1964	29	121
3817-18	40.80	8	1964	110	377
3819-20	40.80	8	1964	720	503
3823-24	40.80	8	1964	44	85
3831-32	50.80	8	1964	29	80
3835-36	40.70	8	1964	23	109
3847-48	40.80	9	1964	328	214
3821-22	40.80	8	1964	361	268

in addition to the normal sources of variation, such as patchiness of plankton, random variations in catch, and errors in the actual counting and subsampling procedures, the estimates incorporate variation in flowmeter performance and average depth over which the oblique tows were made. More important than these factors, however, is the fact that the analysis is based not upon paired hauls, but upon replicates. Replication was necessary because of the limitations of the winch used during the work. One sample was taken while the vessel traveled in a given direction and the other while the vessel moved over the station in the reverse direction. Such a sampling method must result in greater variability than would be obtained from simultaneous hauls.

Errors involved in integrating estimates over time and space have been discussed by a number of authors; the reader is referred to the works of Taft (1960), Saville (1964), and English (1964).

TABLE 2.—Summary of analysis of variance of estimates of abundance of protozoal *Penaeus duorarum* under 10 m.² surface area on the Tortugas Shelf, Florida, August 1962 to October 1964

Source of variation	Degrees of freedom	Sum of squares	Mean square	F ¹
Between stations.....	46	20.087	0.43667	5.97
Between replicate estimates.....	47	3.440	.07319	
Totals.....	93	23.527		

¹ The large value of F indicates that significantly more of the total variation is due to differences between stations than between replicates ($P < 0.01$).

On four occasions during this investigation, several sampling stations were occupied over 24-hour periods. No consistent differences were observed between night and daytime catches, and variability appeared to be within the margins expected according to the foregoing analysis. The oblique-tow method apparently sampled all layers of the water column and counteracted sampling problems caused by diurnal vertical migrations.

SEASONAL ABUNDANCE OF LARVAE

The equation developed for Pacific sardine by Sette and Ahlstrom (1948) and Ahlstrom (1954) has been applied to the counts of first protozoae of *P. duorarum* to obtain estimates of larval production in the sampling area during the period covered by this survey.

The equation is $C = \sum (C_i W_i t_i)$, in which

C = the total number of first protozoae produced in the survey area during the period t_i

$C_i = L_i/D$

L_i = estimated number of first protozoae per 10 m.² of surface area at the i th station

D = the duration of the first protozoal stage (3 days)

W_i = the area represented by station i

t_i = the time weighting given to station i (equal to one-half the time elapsing since the preceding occupancy plus one-half the time elapsing before the succeeding occupancy)

The basic data for the analysis are given in tables 3 and 4. The area represented by each sampling station is 320 km.² (see Sette and Ahlstrom, 1948, for rationale regarding the area represented by a station) and the time weighting, t_i , is usually about 14 days.

The result of the application of the equation is a minimum estimate of total larval production, because the fraction of larvae surviving the period between spawning and metamorphosis to first protozoae (about 3.5 days, according to Ewald, 1965) is unknown. Results of the analysis are given in table 5 and illustrated in figure 2.

The only complete year for which data are available is 1963. We estimated that $60,500 \times 10^8$ first protozoae were produced. It is clear from figure 2, however, that 1963 was a poor year; fewer larvae appear to have been produced than in either 1962 or 1964. If equal weighting is allowed for all data, annual production is in the order of $87,000 \times 10^8$ first protozoae.

SEASONAL VARIATIONS IN SPAWNING INTENSITY

The percentage of the annual catch of protozoae taken in each month from 1959 to 1964 is shown in figure 3. The data are for samples taken between 18.4 and 36.7 m. (10 and 20 fathoms). Data for

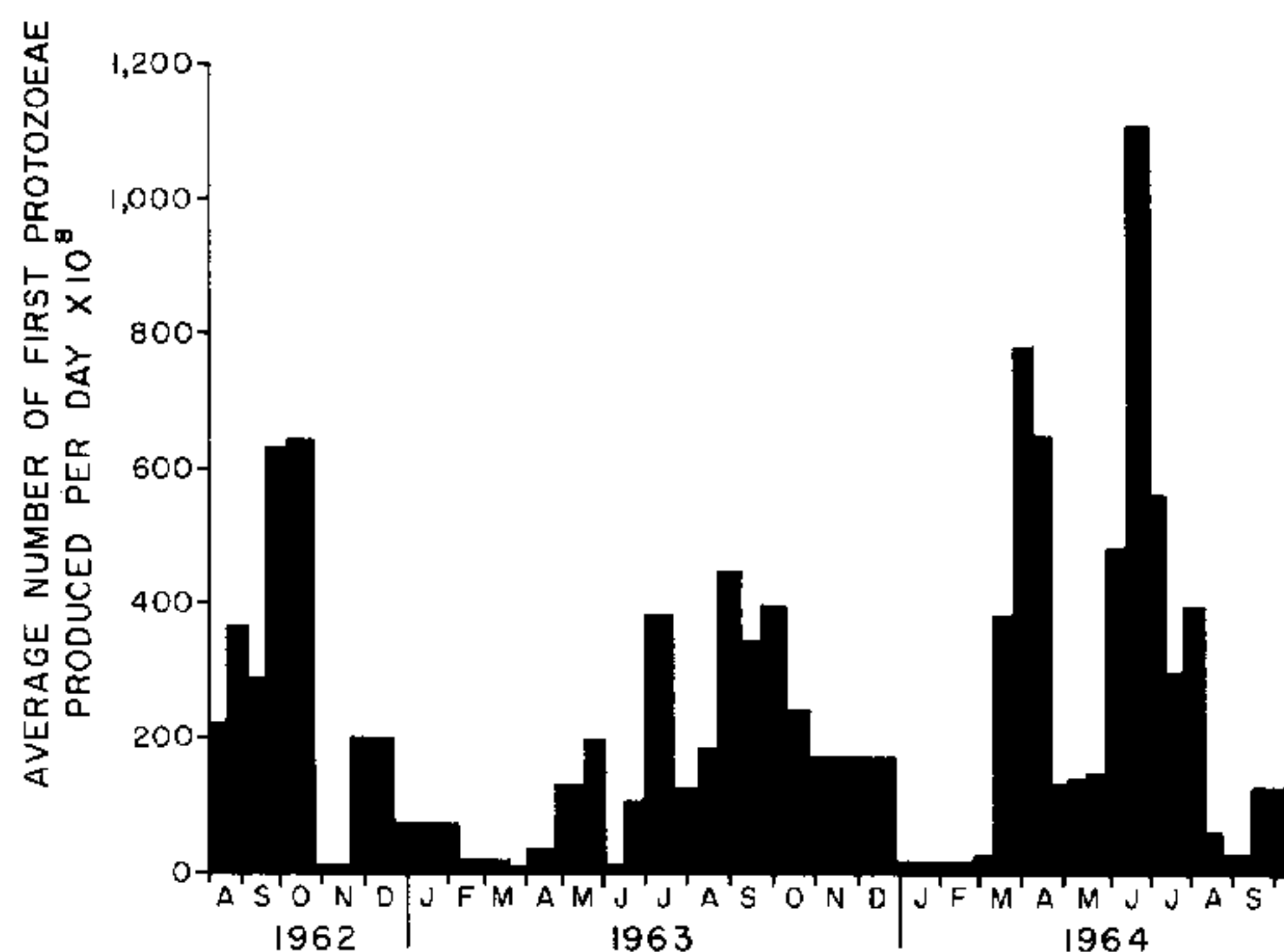


FIGURE 2.—Seasonal fluctuations in production of first protozoae of *P. duorarum* in the Tortugas Shelf area, August 1962 to October 1964.

1959 through mid-1962 are taken from Jones et al. (footnote 6) and are for catches made with the Discovery net; the more recent data are derived from the use of the Gulf V sampler. Because of

TABLE 3.—Summary of Tortugas tows: Cruise totals and physical data. All values are the sum of the computed numbers of *P. duorarum* larvae under 10 m.² surface area at 10 stations on the Tortugas Shelf, August 1962 to October 1964

Cruise	Date	Subtotal by stage				Total	Percentage by stages				Average number of larvae/tow	Moon age	Average bottom temperature
		Protozoae	Myses	Postlarvae			Protozoae	Myses	Postlarvae				
				1-3 spines	4+ spines				1-3 spines	4+ spines			
	1962	Number	Number	Number	Number	Number	Percent	Percent	Percent	Percent	Number	Days	° C.
6201	8/14-16	3,146.1	136.8	129.4	0	3,412.3	92.2	4.1	3.7	0	379.1	16	-----
6202	8/28-30	5,342.3	151.2	106.6	5.3	5,605.4	95.3	2.7	1.9	.1	560.5	29	26.8
6203	9/11-12	6,408.5	612.3	308.8	5.8	7,335.4	87.4	8.3	4.2	.1	733.5	13	26.2
6204	9/25-28	7,448.2	510.7	124.8	3.0	8,086.7	92.1	6.3	1.5	.1	808.7	28	28.7
6205	10/9 -10	8,363.4	434.7	227.9	2.6	9,028.6	92.6	4.8	2.5	.1	902.9	12	28.7
6206	11/7 -8	103.6	3.9	19.5	16.1	143.1	72.4	2.7	13.6	11.3	17.8	11	24.6
6207	12/4 -5	1,923.8	52.0	0	0	1,975.8	97.4	2.6	.3	0	197.6	8	22.8
1963													
6301	1/9 -10	834.2	36.0	28.4	1.7	900.3	92.7	4.0	3.2	.2	90.0	14	20.2
6303	3/11-12	339.8	3.9	0	0	343.7	98.9	1.1	0	0	34.4	16	20.7
6304	3/26-27	126.6	11.3	6.3	0	144.2	87.8	7.8	4.4	0	14.4	2	21.1
6305	4/8 -10	472.3	0	2.5	0	474.8	99.6	0	.4	0	47.5	16	20.9
6306	5/7 -9	1,692.4	104.9	24.9	0	1,822.2	92.8	5.8	1.4	0	182.2	16	23.2
6307	5/20-23	2,638.6	93.0	60.4	0	2,792.0	94.5	3.3	2.2	0	279.2	29	23.1
6308	6/4 -5	198.7	73.3	91.5	7.7	371.2	53.6	19.7	24.6	.1	41.2	13	22.6
6309	6/18-22	1,905.1	391.3	115.2	0	2,411.6	79.0	16.2	4.8	0	241.2	28	23.8
6310	7/1 -2	5,281.2	304.1	23.6	0	5,608.9	94.2	5.4	4.2	0	560.9	11	24.7
6311	7/30-8/1	2,823.2	935.8	1,188.4	28.0	4,975.4	56.7	18.8	23.9	.6	497.5	12	29.6
6313	8/13-14	2,868.4	221.5	411.7	0	3,501.6	81.9	6.3	11.8	0	350.2	25	29.9
6314	8/27-28	9,825.5	1,219.1	341.8	0	11,386.5	86.3	10.7	3.0	0	1,138.7	9	30.1
6315	9/10-11	5,929.8	927.7	314.3	0	7,171.8	82.7	12.9	4.4	0	717.2	23	30.2
6316	10/1 -2	1,380.9	1,793.6	612.7	0	9,787.2	75.4	18.3	6.3	0	978.7	15	28.9
6317	10/15-16	2,604.9	51.7	16.9	14.7	2,688.2	96.9	1.9	.6	.6	268.8	29	29.0
6318	11/5 -6	3,460.1	85.3	56.8	0	3,602.2	96.0	2.4	1.6	0	360.2	20	24.9
1964													
6401	2/17-18	131.2	39.6	0	0	170.8	76.8	23.2	0	0	21.4	5	19.1
6402	3/3 -4	349.8	0	0	0	349.8	100.0	0	0	0	35.0	20	19.5
6403	3/17-18	6,389.1	277.1	6.4	0	6,672.6	95.8	4.2	.1	0	667.3	4	20.5
6404	4/1 -2	16,280.3	4,198.0	1,106.5	4.5	21,589.3	75.5	19.5	5.1	.1	2,158.9	19	22.1
6405	4/14-15	8,483.8	272.0	178.9	2.0	8,936.7	95.0	3.1	2.0	.1	893.7	3	23.4
6406	4/28-30	1,599.8	147.6	196.3	0	1,943.7	82.2	7.6	10.2	0	194.4	17	24.7
6407	5/12-14	1,721.2	137.9	79.9	8.5	1,947.5	88.4	7.1	4.1	.4	194.8	2	26.2
6408	5/26-28	2,242.8	324.8	149.0	0	2,716.6	82.6	12.0	5.5	0	273.6	16	26.9
6409	6/9 -11	7,225.6	409.6	89.9	0	7,725.1	93.5	5.3	1.2	0	772.5	1	27.6
6410	6/23-25	21,404.9	1,582.7	762.6	16.3	23,766.5	90.2	6.7	3.2	.1	2,376.7	14	27.1
6411	7/7 -9	9,739.7	444.0	360.9	0	10,544.6	92.4	4.2	3.4	0	1,054.5	28	28.3
6412	7/21-23	4,846.2	711.4	518.6	6.6	6,082.8	79.6	11.7	8.5	.1	608.3	13	28.3
6413	8/4 -5	5,887.0	406.5	304.2	4.8	6,602.7	89.2	6.2	4.6	.1	660.3	24	28.6
6414	8/18-21	1,207.9	146.8	38.6	0	1,393.3	86.7	10.5	2.8	0	139.3	12	25.5
6415	9/1 -2	343.0	7.6	50.3	0	400.9	85.5	1.9	12.5	0	40.0	22	22.9
6416	10/2 -6	1,725.8	38.9	9.3	0	1,774.0	97.3	2.2	.5	0	177.4	28	25.0

TABLE 4.—Summary of Tortugas tows: Cruise totals by stage. All values are the sum of the computed numbers of each larval stage of *P. duorarum* under 10 m.² surface area at 10 stations on the Tortugas Shelf,¹ August 1962 to October 1964

Year and cruise number	Stage										
	Protozoae			Myses			Postlarvae				
	1	2	3	1	2	3	1	2	3	4	5
1962	Number	Number	Number	Number	Number	Number	Number	Number	Number	Number	Number
6201	1,669.7	995.6	480.8	43.4	34.6	58.8	46.8	57.1	25.5	0	0
6202	3,201.8	1,384.3	756.2	75.5	19.0	56.7	48.1	36.3	22.2	5.3	0
6203	2,465.1	2,473.6	1,469.8	281.3	166.9	164.1	214.5	59.0	35.3	5.8	0
6204	5,508.0	1,575.7	364.5	288.4	83.4	138.9	50.4	41.5	32.9	3.0	0
6205	5,580.3	1,922.4	880.7	300.4	66.3	68.0	93.3	92.4	42.2	2.6	0
6206	64.0	39.6	0	0	0	3.9	16.2	0	7.0	16.1	0
6207	1,741.9	154.7	27.2	33.1	18.9	0	0	0	0	0	0
1963											
6301	628.3	132.3	73.6	15.6	12.6	7.8	20.2	4.1	4.1	1.7	0
6303	171.2	101.7	66.9	3.9	0	0	0	0	0	0	0
6304	63.7	37.2	25.7	11.3	0	0	2.1	2.1	2.1	0	0
6305	322.4	136.3	13.6	0	0	0	0	0	2.5	0	0
6306	1,119.1	418.0	155.3	41.7	0	63.2	24.9	0	0	0	0
6307	1,757.5	635.5	245.6	50.7	12.7	29.6	26.5	21.0	12.9	0	0
6308	93.3	46.0	59.4	23.5	6.6	43.2	21.2	52.3	18.0	5.1	2.6
6309	902.3	660.7	342.1	188.9	20.5	181.9	103.7	11.5	0	0	0
6310	3,346.6	1,501.9	432.7	210.4	46.4	47.3	11.8	6.8	5.0	0	0
6311	1,105.2	1,202.0	516.0	254.3	211.9	469.6	879.7	218.4	90.3	28.0	0
6313	1,633.3	614.4	620.7	138.8	24.1	58.6	44.5	267.3	99.9	0	0
6314	3,943.0	3,154.1	2,728.4	602.8	309.2	307.2	126.3	206.5	9.0	0	0
6315	2,976.5	1,682.8	1,270.5	631.6	120.8	175.3	208.1	82.6	23.6	0	0
6316	3,463.5	2,442.2	1,475.2	716.0	372.4	705.2	399.6	185.7	27.4	0	0
6317	2,126.2	244.0	234.7	40.4	11.3	0	5.7	5.6	5.6	14.7	0
6318	1,737.2	1,444.2	278.7	65.0	6.4	13.9	28.0	28.8	0	0	0
1964											
6401	126.9	4.3	0	12.8	6.6	20.2	0	0	0	0	0
6402	202.9	88.0	58.9	0	0	0	0	0	0	0	0
6403	3,348.6	2,190.4	850.1	185.2	53.4	38.5	6.4	0	0	0	0
6404	6,831.7	5,368.3	4,080.3	2,051.1	921.9	1,225.0	663.2	400.2	43.1	4.5	0
6405	5,662.2	2,146.4	675.2	90.4	66.3	115.3	55.3	96.7	26.9	2.0	0
6406	1,087.9	406.0	105.9	37.3	20.7	89.6	80.1	116.2	0	0	0
6407	1,219.6	361.0	140.6	69.8	38.3	29.8	11.3	32.6	36.0	8.5	0
6408	1,291.2	734.9	216.7	180.3	20.4	124.1	97.5	44.7	6.8	0	0
6409	4,210.7	1,882.9	1,132.0	228.4	103.1	78.1	38.7	51.2	0	0	0
6410	9,665.8	8,077.4	3,661.7	749.0	333.3	500.4	478.0	233.2	51.4	16.3	0
6411	4,885.3	3,195.6	1,658.8	232.2	105.4	106.4	222.1	95.4	43.4	0	0
6412	2,550.6	1,422.2	873.4	322.1	121.8	267.5	244.2	225.5	48.9	6.6	0
6413	3,447.4	1,801.0	638.6	138.8	126.2	141.5	197.0	75.4	31.8	4.8	0
6414	498.9	479.9	229.1	58.2	64.5	24.1	33.6	5.0	0	0	0
6415	206.4	72.7	63.9	3.8	3.8	0	0	50.3	0	0	0
6416	1,109.2	371.0	245.7	14.7	24.2	0	9.3	0	0	0	0

¹ The totals for cruises 6201, 6206, 6308, and 6401 are the sums of 9, 8, 9, and 8 stations, respectively.

the different sampling characteristics of the two nets, data for the first and second halves of 1962 cannot strictly be compared. The average catch of the Gulf V net per unit volume of water strained during the spawning seasons of 1963 and 1964 was about 10 times greater than the catch of the Discovery net during the spawning seasons of 1959-61. In the construction of the histograms for 1962, the numbers per 1,000 m.³ filtered by the Discovery net have been equated with the numbers per 100 m.³ filtered by the Gulf V net.

Spawning occurred throughout the annual temperature range of 19° C. to 30° C., but most spawning occurred when temperatures exceeded 25° C. and peaks were usually associated with the highest temperatures reached in each year. Highest temperatures were recorded as early as June and as late as the end of September, resulting in corresponding shifts from year to year in the main time of spawning.

SEASONAL RELATION BETWEEN DEPTH AND SPAWNING

In general, a seasonal shift was observed in the depth at which most spawning (as measured by the presence of first protozoa) occurred. The center of abundance of first protozoa was usually at the shallowest stations in early spring and then moved toward deeper water as the season progressed until in the fall it was at depths greater than 30 m. (16.7 fathoms). In 1962 the center of abundance of first protozoa moved from about 25 m. (13.8 fathoms) in August and September to about 32 m. (17.7 fathoms) by early November (fig. 4). In 1963 a steady movement of the center of spawning was again apparent from the shallow waters (20 to 25 m. or 11.1 to 13.8 fathoms) in early spring to a depth of 36 m. (20 fathoms) in early November. This movement was not as apparent in 1964, possibly because maximum spawning occurred earlier in the year.

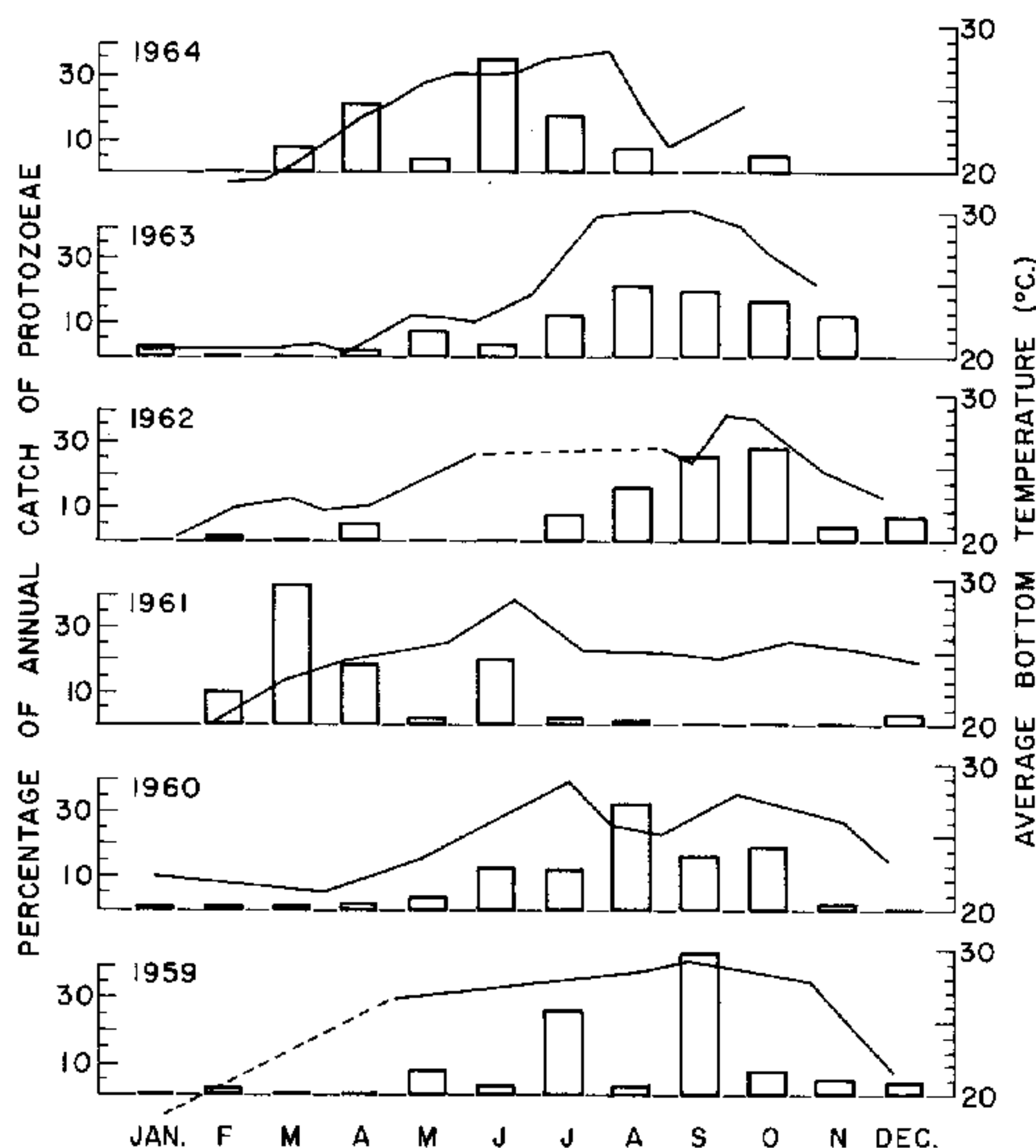


FIGURE 3.—Histograms showing the relation between the percentage of the annual catch of first protozoae taken in each month, and (solid lines) the average bottom water temperature from the Tortugas Shelf area, 1959–64. Broken lines indicate no data.

An analysis of the distribution of bottom temperatures suggests that temperature plays no significant part in the movement of the center of spawning. During 1963, when the movement into deeper water was most marked, bottom temperatures appeared to be almost uniform at any given time throughout the sampling area. Shrimp landing data for 1963 (U.S. Fish and Wildlife Service, 1964) showed that small shrimp appeared in the shallow areas of the trawling grounds about April and again in October. Previous studies of adult shrimp (Iversen and Jones, 1961; Iversen, Jones, and Idyll, 1960; and Iversen and Idyll, 1959) have shown that the average size of shrimp increases with increasing depth. Shrimp tagging studies also have indicated a migration toward deeper water. Apparently the maturing shrimp entering the fishery in the early part of the summer begin spawning when they reach a suitable size and continue to spawn as they migrate to deeper water. This theory is compatible with data on maturation and growth provided by Eldred, Ingle, Woodburn, Hutton, and Jones (1961) and by Iversen (1962).

TABLE 5.—Estimates of the production of first protozoae of *P. duorarum* on the Tortugas Shelf, August 1962 to October 1964

Cruise	Date	Length of inter-cruise period	First proto-zoae produced during inter-cruise period	Average number of first protozoae produced per day
<i>1962</i>				
6201	Aug. 14–16	14.0	2,993.0	213.8
6202	Aug. 28–30	13.8	5,091.9	369.0
6203	Sept. 11–12	14.3	4,062.2	284.1
6204	Sept. 25–28	14.0	8,886.2	634.7
6205	Oct. 9–10	21.0	13,455.5	640.7
6206	Nov. 7–8	28.0	258.5	9.2
6207	Dec. 4–5	32.0	6,423.0	200.7
<i>1963</i>				
6301	Jan. 9–10	48.5	3,511.0	72.4
6303	Mar. 11–12	38.0	750.1	19.7
6304	Mar. 26–27	14.3	104.8	7.3
6305	Apr. 8–10	21.3	791.6	37.2
6306	May 7–9	21.3	2,746.6	129.0
6307	May 20–23	13.8	2,794.7	202.5
6308	June 4–5	14.8	177.0	12.0
6309	June 18–22	13.5	1,403.9	104.0
6310	July 1–2	20.8	8,021.3	385.6
6311	July 30–Aug. 1	21.5	2,738.2	127.4
6313	Aug. 13–14	13.5	2,540.8	188.2
6314	Aug. 27–28	13.5	6,134.0	454.4
6315	Sept. 9–10	17.5	6,002.7	343.0
6316	Oct. 1–2	18.0	7,184.2	399.1
6317	Oct. 15–16	17.5	4,287.6	245.0
6318	Nov. 5–6	64.5	11,352.1	176.0
<i>1964</i>				
6401	Feb. 17–18	59.0	1,079.0	18.3
6402	Mar. 3–4	14.0	327.2	23.4
6403	Mar. 17–18	14.5	5,595.3	385.9
6404	Apr. 1–2	14.0	11,021.5	787.3
6405	Apr. 14–15	13.8	9,004.4	652.5
6406	Apr. 28–30	14.3	1,792.6	125.4
6407	May 12–14	14.0	1,967.4	140.5
6408	May 26–28	14.0	2,083.1	148.8
6409	June 9–11	14.0	6,793.4	485.2
6410	June 23–25	14.0	15,593.8	1,113.8
6411	July 7–9	14.0	7,881.4	563.0
6412	July 21–23	13.8	4,056.2	293.9
6413	Aug. 4–5	14.3	5,680.8	397.3
6414	Aug. 18–21	14.0	804.9	57.5
6415	Sept. 1–2	22.3	530.4	23.8
6416	Oct. 2–4	30.0	3,834.3	127.8

INTRAMONTHLY VARIATIONS IN SPAWNING—THE EFFECT OF MOON PHASE

The percentage of various larval stages in the total catch varied considerably on successive cruises. We analyzed these variations to determine whether they could in some way be related to the lunar phases.

The percentage which first protozoae represented in the total catch of larvae and postlarvae taken on each cruise was calculated and plotted against moon age minus 5 days (table 6). The average age of first protozoae is 5 days (Ewald, 1965), and subtracting 5 days backdates the observation of the relative abundance of protozoae to the time of spawning. The average of the percentages of protozoae in all catches was 50.6 percent; in 12 of 18 catches taken during the waxing moon (0–14.7 days) the relative abundance of first protozoae was below average (fig. 5), whereas in 11 of 17 catches during the waning moon the relative abundance was above average.

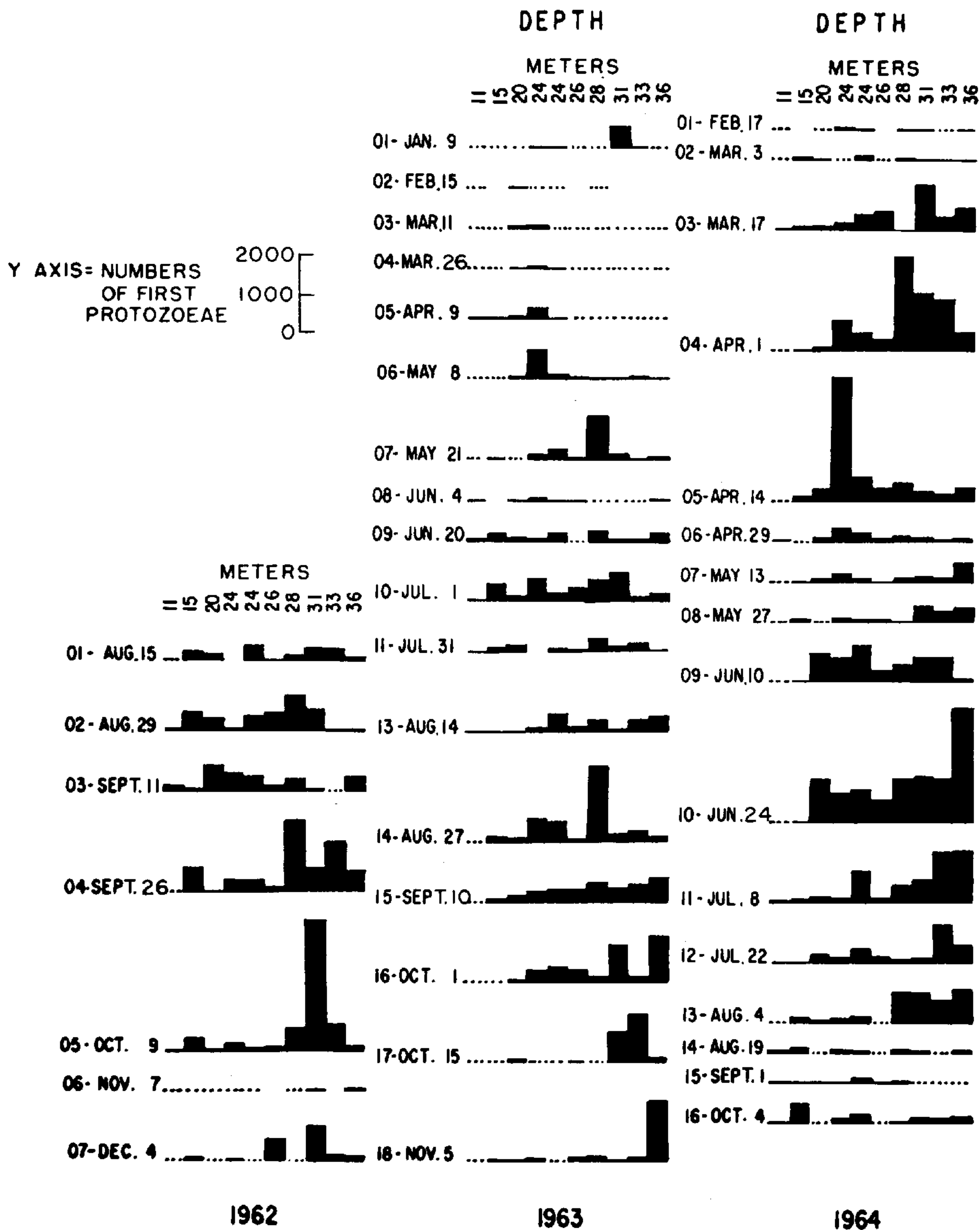


FIGURE 4.—Histograms showing the seasonal movement of the center of abundance of first protozoae of *P. duorarum* from shallow-water stations toward deepwater stations, Tortugas Shelf, Fla., August 1962 to October 1964. Numbers preceding dates indicate cruise numbers.

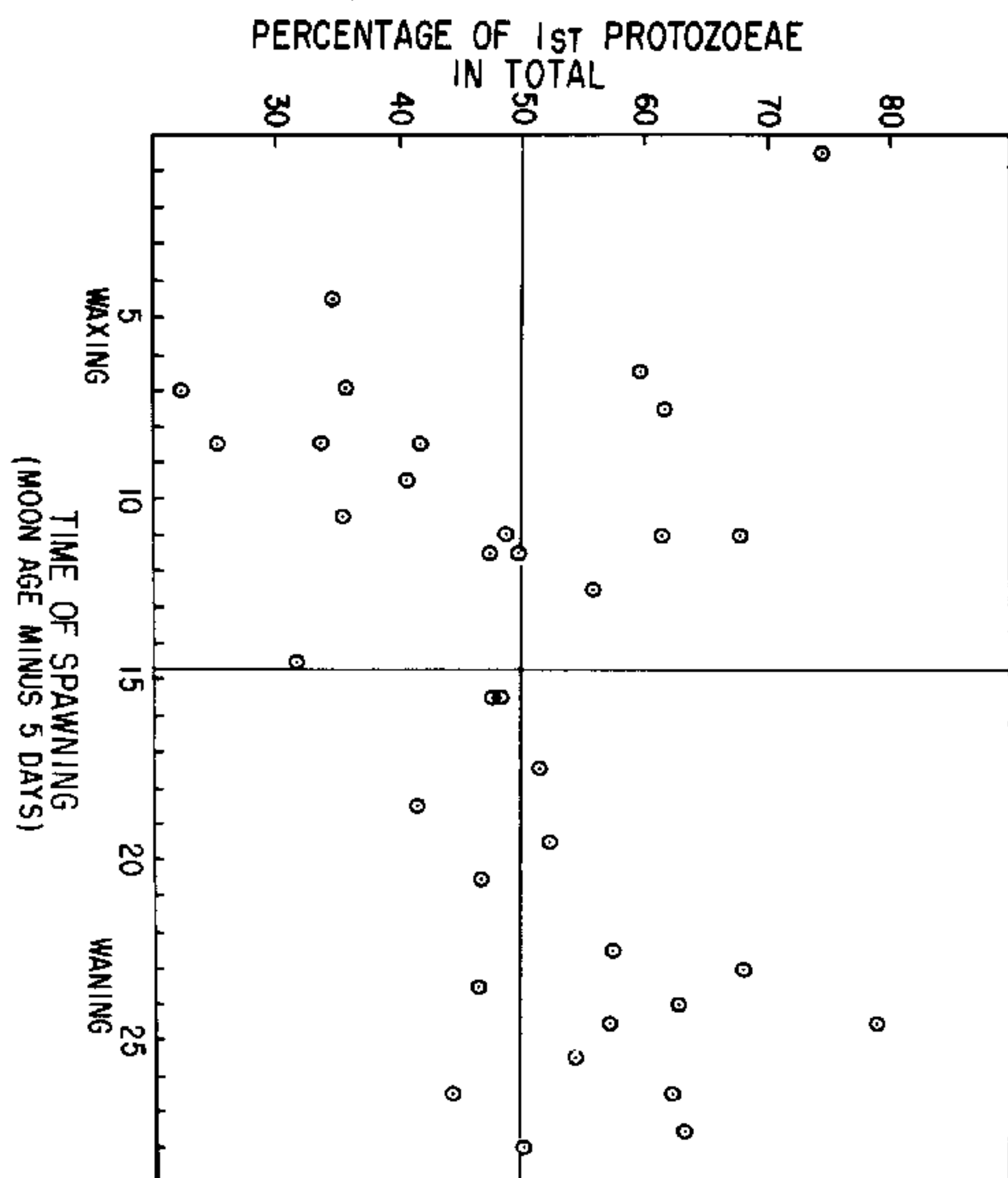


FIGURE 5.—The relation between moon phase and relative spawning intensity (as measured by the relative abundance of first protozoae) in the Tortugas Shelf area, August 1962 to October 1964.

Using a chi-square test, we found that the probability of such a distribution arising by chance is slight (<0.02); we conclude, therefore, that spawning occurs mainly during the last half of the lunar month. That most spawning occurs in the last half of the lunar month agrees with the observations of Korringa (1957), who stated that in animals showing lunar periodicity in spawning, the spawning is often concentrated around the last lunar quarter. He suggested that this concentration is a result of a photoperiodic effect, the final stages of maturation of the gonads being triggered by the greater exposure to light during the full-moon period. This photoperiodic effect on maturation may also hold for *Penaeus*, but the advantages of lunar periodicity are obscure because copulation occurs in advance of spawning (Hudinaga, 1942, for *P. japonicus*), and all eggs are fertilized at extrusion. Alternating periods of high and low larval density may be advantageous in that they prevent a concentrating of major predators, thus reducing mortality caused by prolonged predation.

TABLE 6.—Data for the analysis of the effect of moon phase on rate of spawning of *P. duorarum*; all data are in terms of estimated numbers of larvae under 10 m.² surface area at 10 stations on the Tortugas Shelf, August 1962 to October 1964

Year and cruise number	Date	First proto-zoeae	Total larvae	Percentage of first protozoeae in total catch	Time of spawning (moon age minus 5 days)
1962					
6201	Aug. 14-16	1,669.7	3,412.3	48.9	10-12
6202	Aug. 28-30	3,201.8	4,605.4	57.1	24-25
6203	Sept. 11-12	2,465.1	7,335.4	33.6	8-9
6204	Sept. 25-28	5,508.0	8,086.7	68.1	22-24
6205	Oct. 9-10	5,560.3	9,028.6	61.6	7-8
1963					
6303	Mar. 11-12	171.2	343.7	49.8	11-12
6304	Mar. 26-27	63.7	144.2	44.2	26-27
6305	Apr. 8-10	322.4	474.8	67.9	10-12
6306	May 5-7	1,119.1	1,822.2	61.4	10-12
6307	May 20-23	1,757.5	2,792.0	62.9	23-25
6308	June 4-5	93.3	371.2	25.1	8-9
6309	June 18-22	1,145.1	2,411.6	57.5	22-23
6310	July 1-2	3,346.6	5,608.9	59.7	6-7
6311	July 30-Aug. 1	1,105.2	4,975.4	22.2	6-8
6313	Aug. 13-14	1,633.3	3,501.6	46.6	20-21
6314	Aug. 27-28	3,943.0	11,386.5	34.6	4-5
6315	Sept. 10-11	2,976.5	7,171.8	41.5	18-19
6316	Oct. 1-2	3,463.5	9,787.2	35.4	10-11
6317	Oct. 15-16	2,126.2	2,688.2	79.1	24-25
6318	Nov. 5-6	1,737.2	3,602.2	48.2	15-16
1964					
6401	Feb. 17-18	126.9	170.8	74.2	0-1
6402	Mar. 3-4	202.9	349.8	58.0	15-16
6403	Mar. 17-18	3,348.6	6,672.6	50.2	27-29
6404	Apr. 1-2	6,831.7	21,589.3	31.6	14-15
6405	Apr. 14-15	5,662.2	8,936.7	63.3	27-28
6406	Apr. 28-30	1,087.9	1,943.7	55.9	12-13
6407	May 12-14	1,219.6	1,947.5	62.2	26-27
6408	May 26-28	1,291.2	2,716.6	47.5	11-12
6409	June 9-11	4,210.7	7,725.1	54.5	25-26
6410	June 23-25	9,665.8	23,766.5	40.7	9-10
6411	July 7-9	4,885.2	10,544.6	46.3	23-24
6412	July 21-23	2,550.6	6,082.8	41.9	8-9
6413	Aug. 4-5	3,447.4	6,602.7	52.2	19-20
6414	Aug. 18-21	498.9	1,393.3	35.8	5-9
6415	Sept. 1-2	206.4	400.9	51.5	17-18

MORTALITY AND MIGRATION

The two factors of larval mortality and migration toward the inshore nursery grounds are inseparable and will be dealt with concurrently. Sampling stations which lie on the migration route will always receive immigrant larvae, and, as a result, survival rates calculated from the catch of larvae at such stations will be higher than the true value; conversely, calculations of survival based upon the catch taken at stations from which larvae consistently emigrate will underestimate the true survival rates.

Totals are given in table 7 of the estimates of numbers of each larval stage under 10 m.² surface area for 37 cruises in the sampling area from August 1962 to July 1964. These estimates provide a measure of the relative abundance of each larval stage for 2 calendar years.

Calculation of survival rates on a temporal basis requires knowledge of the duration of the various larval stages. The following figures for the

average time spent in each larval stage have been derived from the information given by Ewald (1965) on the rate of development of larvae at 26° C.:

	Stage	Days
Egg	-----	1.5
Nauplius	-----	2.0
1st protozoa	-----	3.0
2d protozoa	-----	2.4
3d protozoa	-----	2.2
1st mysis	-----	2.0
2d mysis	-----	2.3
3d mysis	-----	3.0
1-spine postlarva	-----	2.0
2-spine postlarva	-----	2.0
3-spine postlarva	-----	3.0
4-spine postlarva	-----	3.0
5-spine postlarva	-----	6.0

Growth and development of larvae in the laboratory may differ considerably from that in the ocean; however, the relative duration of the instars may be expected to be nearly constant, and in the absence of better data the times given above have been used to plot catch curves for the larvae.

Catch curves, obtained by plotting the logarithm of the total "catch" of each stage against the estimated average age of the larval stage, are shown in figure 6. A feature common to all of the curves is that the catch of first and second mysids appears to have been depressed. At all stations, the catch of second mysids was less than the catch of third mysids. Several possible explanations for this depression of the catch curve present themselves.

First, it is possible that the larvae are most active in the first and second mysis stages, and that the depressed catch of these stages reflects active avoidance of the Gulf V net. Heldt (1938)

TABLE 7.—Totals of the estimates of numbers of each larval stage of *P. duorarum* under 10 m.² surface area for 37 cruises in the Tortugas Shelf area, August 1962 to July 1964

Station	Depth	Protozoae			Myses			Postlarvae		
		1	2	3	1	2	3	1	2	3
	<i>M.</i>				<i>Number</i>					
50.100	36.5	<i>12,618</i>	<i>5,420</i>	<i>2,307</i>	<i>591</i>	<i>241</i>	<i>452</i>	<i>355</i>	<i>43</i>	<i>17</i>
50.90	33.0	<i>11,350</i>	<i>5,704</i>	<i>3,221</i>	<i>1,037</i>	<i>263</i>	<i>556</i>	<i>209</i>	<i>150</i>	<i>0</i>
50.80	31.0	<i>16,040</i>	<i>7,497</i>	<i>3,151</i>	<i>1,039</i>	<i>339</i>	<i>520</i>	<i>355</i>	<i>146</i>	<i>6</i>
40.90	27.5	<i>14,008</i>	<i>6,438</i>	<i>2,910</i>	<i>1,054</i>	<i>272</i>	<i>451</i>	<i>182</i>	<i>195</i>	<i>17</i>
50.70	25.5	<i>5,020</i>	<i>2,841</i>	<i>2,145</i>	<i>972</i>	<i>434</i>	<i>477</i>	<i>436</i>	<i>364</i>	<i>180</i>
40.80	24.0	<i>8,572</i>	<i>6,841</i>	<i>6,087</i>	<i>1,194</i>	<i>604</i>	<i>955</i>	<i>546</i>	<i>541</i>	<i>37</i>
40.70	24.0	<i>10,579</i>	<i>7,232</i>	<i>4,108</i>	<i>949</i>	<i>442</i>	<i>786</i>	<i>564</i>	<i>428</i>	<i>123</i>
40.60	20.0	<i>5,112</i>	<i>4,824</i>	<i>1,848</i>	<i>1,440</i>	<i>506</i>	<i>785</i>	<i>1,263</i>	<i>367</i>	<i>117</i>
32.70	14.5	<i>3,324</i>	<i>1,474</i>	<i>783</i>	<i>345</i>	<i>127</i>	<i>150</i>	<i>159</i>	<i>193</i>	<i>102</i>
30.58	11.0	<i>279</i>	<i>472</i>	<i>438</i>	<i>215</i>	<i>60</i>	<i>152</i>	<i>204</i>	<i>244</i>	<i>241</i>

NOTE. The five highest values in each column are in *italic*.

has stated that the mysids appear to be the most active larval stages.

Secondly, third mysids and older postlarvae spawned in another area (possibly to the north of the Tortugas) may drift into the Tortugas area, thus increasing the catch of the stages older than second mysis. Jones et al. (footnote 6), however, reported no evidence of any other center of spawning.

Finally, an error in the estimated time required for the shrimp to develop through the mysis stages may account for this discrepancy. Since mysis stages are rather ill-defined, allocation to first, second, or third mysis may be somewhat arbitrary, depending upon the degree of development of the pleopods and telson. More than three stages may exist at temperatures lower than 26° C. (Ewald, 1965). If average duration of mysis stages is less than the postulated 7.3 days, then the daily survival rate must decrease considerably after the third protozoal stage and then increase again during the postlarval stages.

The first alternative—avoidance of the net—suggested above is considered to be most likely. An inspection of the catch curves shows that the slope of the curves during the protozoal stages and during the stages subsequent to third mysis is fairly uniform; in a number of catch curves, the points describing the abundance of the third protozoal stage and of the third mysis stage can be joined to produce an almost uniform slope throughout the catch curve (fig. 6). This view is also supported by the work of Jones et al. (footnote 6), who found that the numbers of larvae decline steadily between the third protozoal stage and the third mysis stage. Jones et al. (footnote 6) used a Discovery net of 76-cm. mouth diameter and with larger mesh sizes than those of the Gulf V sampler. Such a net may capture a more representative proportion of the highly motile stages than the faster moving but smaller Gulf V sampler (Barkley, 1964).

The slopes of the catch curves shown in figure 6 appear to vary. For comparing these apparent variations in survival, we have calculated the gross survival between selected stages for each of the 10 stations. Distributions of gross survival values between first and third protozoae, third protozoae and third mysids, and third mysids and two-spine postlarvae are plotted in figure 7a, b, and c. Choice of these stages for the calculations was dictated by the anomalies that appeared

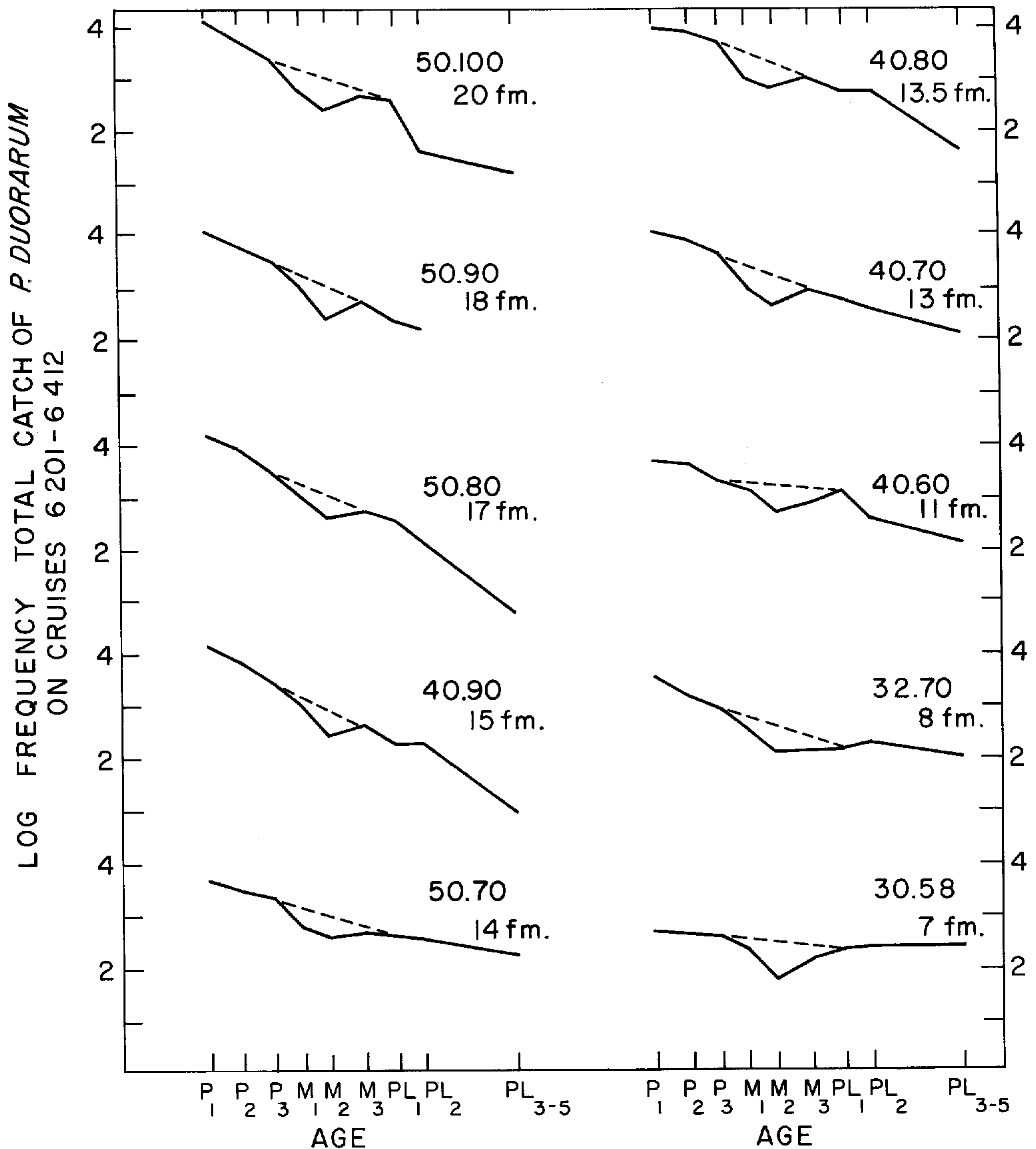


FIGURE 6.—Catch curves for larvae and postlarvae of *P. duorarum* based on the total catch at 10 stations on the Tortugas Shelf, August 1962 to October 1964. P_1 , P_2 , P_3 =1st, 2d, and 3d protozoal stages; M_1 , M_2 , M_3 =1st, 2d, and 3d mysis stages; PL_1 , PL_2 , PL_{3+5} =1-, 2-, and 3- to 5-spine postlarval stages. Stages are distributed along abscissa relative to the mean age of each larval stage.

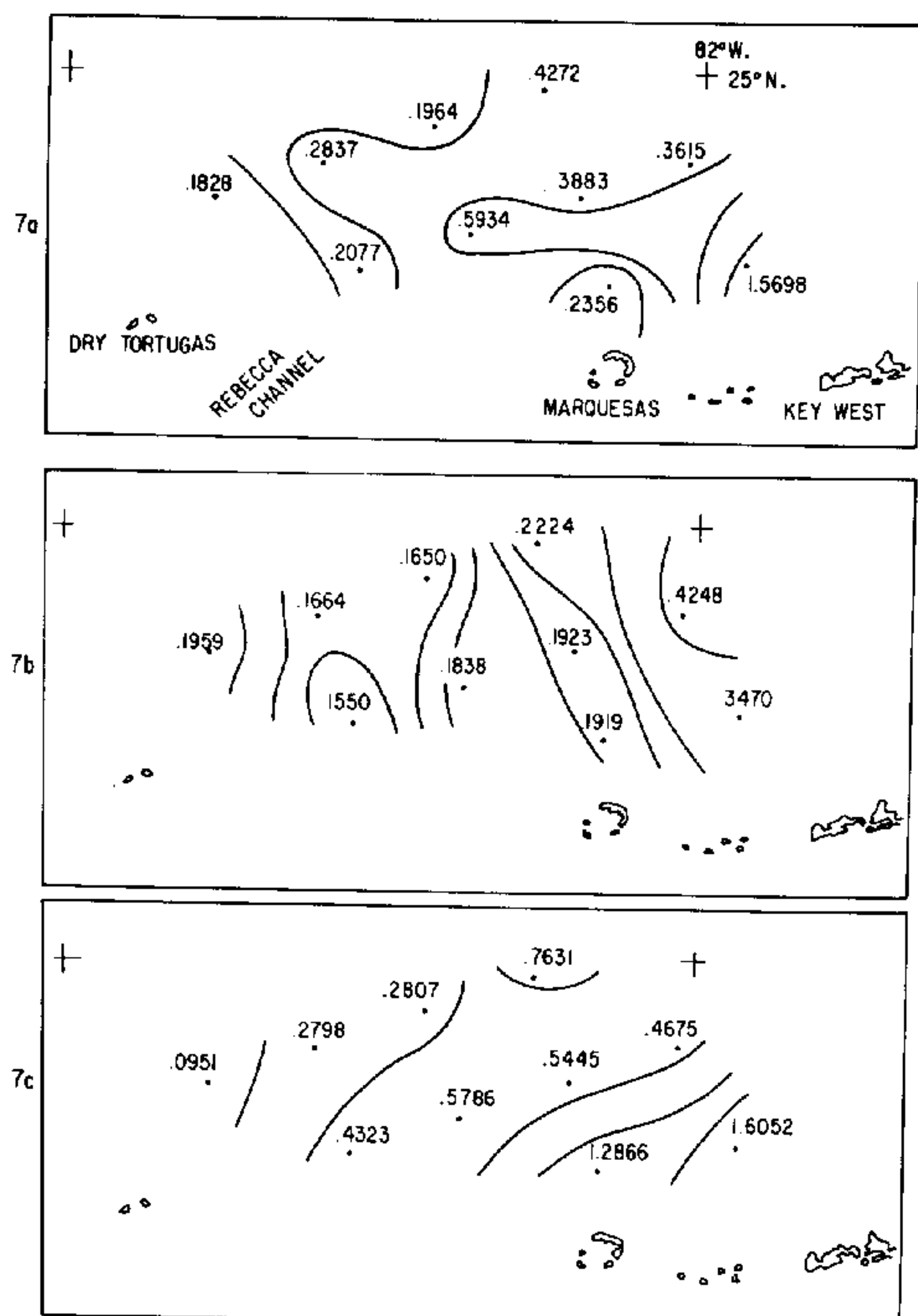


FIGURE 7a, b, and c.—Variations in apparent gross survival of larval and postlarval *P. duorarum* at 10 sampling stations on the Tortugas Shelf, August 1962 to October 1964: (a) 1st protozoal to 3d protozoal stage, (b) 3d protozoal to 3d mysis stage, and (c) 3d mysis to 2-spine postlarval stages.

in the catch curves and which have been discussed above. Lowest apparent survival was consistently in the deepwater stations in the northwestern sector of the sampling area, and greatest apparent survival (in some cases exceeding 100 percent) was in the southeastern sector. It appears highly unlikely that the calculated values are real values and that survival of larvae is greater in the southeastern sector. These consistent differences are probably a result of the migration of larvae away from the center of spawning. Stations 40.90 and 50.80 are believed to represent the centers of spawning, and the larvae disperse from this center.

Calculated daily survival rates between successive larval stages at each of the 10 stations are given in table 8. Total survival between first

protozoal and one-spined postlarval stages also is given (right-hand column); the highest rate of survival between these stages is usually at the shallowest, more easterly stations (fig. 8).

Because the dispersal of larvae from the center of spawning appears to affect the survival estimates pertaining to specific stations, it is difficult to estimate the true survival rate. Calculations of survival rate based upon the total catch of successive stages in relation to the total catch of first protozoae will have validity, however, provided it can be assumed that the main route of dispersal is over the area covered by the sampling stations (table 9).

If estimates of survival rates between first protozoa and first and second mysis are discarded, all remaining estimates are nearly constant and range from 78.6 to 82.0 percent (mean, 80.4 percent) per day.

Postlarvae enter the Everglades nursery grounds in the six-spine stage (Tabb, Dubrow, and Jones, 1962). On the basis of age data provided by Ewald (1965), these larvae are about 35 days old. At a survival rate of 80.4 percent per day, the fraction of the original population which survives to enter the nursery grounds can be estimated at 0.804^{35} , or 0.05 percent. The fraction of the original population of first protozoae (average age 5 days)

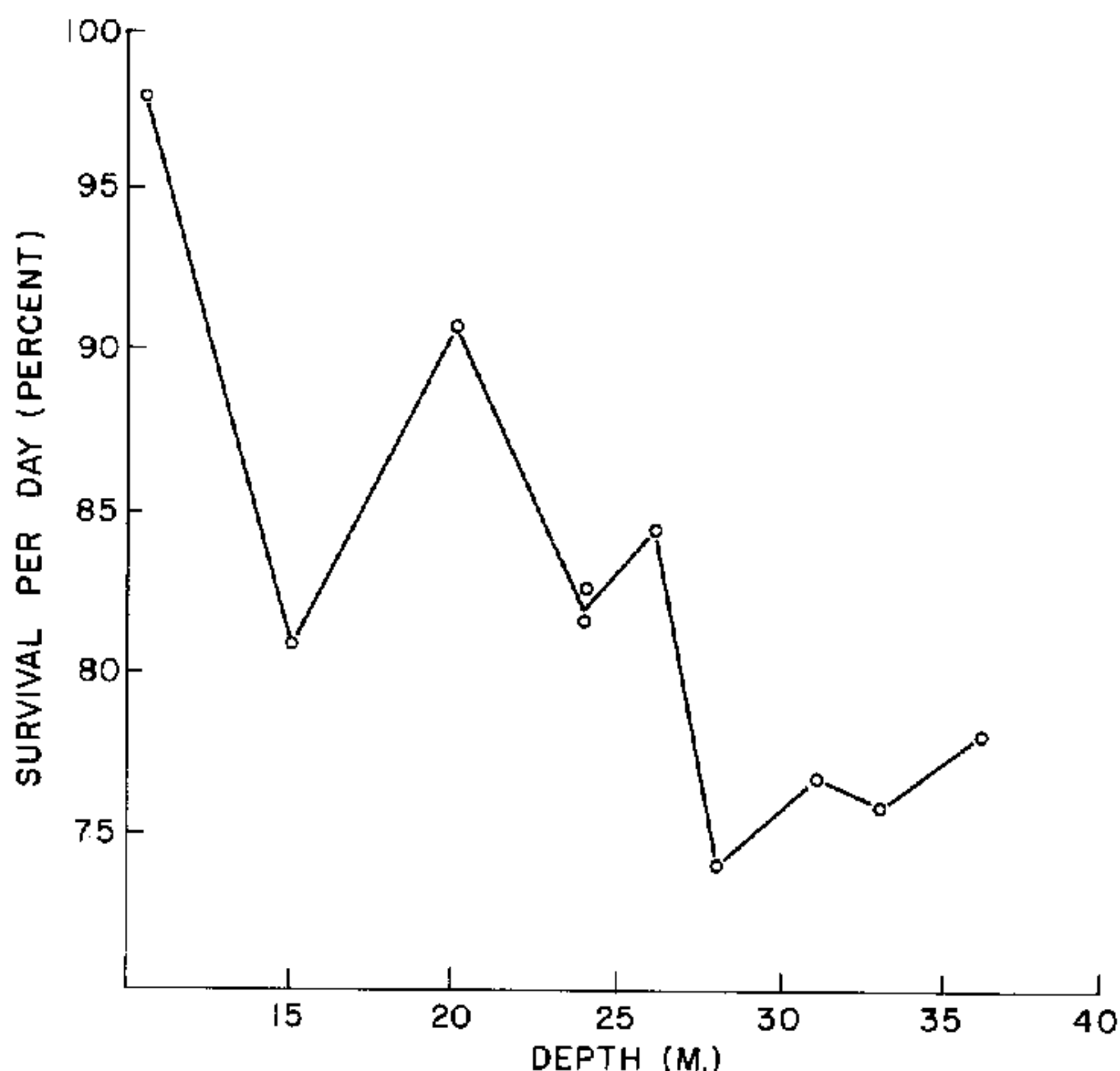


FIGURE 8.—The relation at 10 sampling stations on the Tortugas Shelf, August 1962 to October 1964, between depth and apparent survival rates of *P. duorarum* between 1st protozoal and 1-spine postlarval stages.

TABLE 8.—Calculated daily survival rates between successive larval and postlarval stages of *P. duorarum* at 10 sampling stations on the Tortugas Shelf

Station	Depth	Stages ¹								
		P ₁ -P ₂	P ₂ -P ₃	P ₃ -M ₁	M ₁ -M ₂	M ₂ -M ₃	M ₃ -Pl ₁	Pl ₁ -Pl ₂	Pl ₂ -Pl ₃₊₅	P ₁ -Pl ₁
	<i>M.</i>	<i>Fractional survival per day</i>								
50.100	36	.7311	.6898	.5228	.6585	1.2690	.9080	.3459	.8752	.7803
50.90	33	.7732	.7800	.5229	.5282	1.3090	.6858	.8468	-----	.7578
50.80	31	.7546	.6860	.5395	.6328	1.1160	.8582	.6409	.6354	.7678
40.90	28	.7496	.7081	.6166	.5330	1.2090	.6963	1.0350	.6884	.7396
50.70	26	.8098	.8849	.5508	.8513	1.0360	.9640	.9139	.9040	.8439
40.80	24	.9198	.8790	.5214	.7382	1.1800	.8067	.9965	.6814	.8269
40.70	24	.8708	.7796	.4977	.7008	1.2430	.8756	.8710	.8370	.8158
40.60	20	.9786	.6589	.8880	.6159	1.1790	1.2090	.5392	.8487	.9072
32.70	15	.7399	.7597	.6769	.6284	1.0650	1.0230	1.1000	.9137	.8098
30.58	11	1.2150	.9683	.7132	.5501	1.4230	1.1250	1.0950	.9979	.9786

¹ P₁, P₂, P₃=1st, 2d, and 3d protozoal stages; M₁, M₂, M₃=1st, 2d, and 3d mysis stages; and Pl₁, Pl₂, Pl₃₊₅=1-, 2-, 3- to 5-spine postlarval stages.

TABLE 9.—Estimated daily survival rates of larval *P. duorarum* over successively longer intervals on the Tortugas Shelf, August 1962 to October 1964

Stages ¹	Duration between stages		Calculated daily survival rate
	Days	Percent	
P ₁ -P ₂	2.70	0.8074	
P ₁ -P ₃	5.00	.7856	
P ₁ -M ₁	7.10	.7247	
P ₁ -M ₂	9.25	.7031	
P ₁ -M ₃	11.90	.7898	
P ₁ -Pl ₁	14.40	.8112	
P ₁ -Pl ₂	16.40	.8087	
P ₁ -Pl ₃₊₅	23.40	.8202	

¹ P₁, P₂, P₃=1st, 2d, and 3d protozoal stages; M₁, M₂, and M₃=1st, 2d, and 3d mysis stages; and Pl₁, Pl₂, Pl₃₊₅=1-, 2-, and 3- to 5-spine postlarval stages.

² Estimates affected by sampling error.

would be 0.804³⁰, or 0.14 percent. In 1963, about 60,500×10⁸ first protozoae were produced within the sampling area; at the postulated rate of survival, about 85×10⁸ six-spine postlarvae would enter the nursery grounds. The total commercial catch of *P. duorarum* adults in the Tortugas area during 1963 was about 500 million individuals (U.S. Fish and Wildlife Service, 1964), implying that about 6 percent of the postlarvae may survive to be captured when they move to the trawling grounds as juveniles and adults.

Owing to the lunar periodicity of spawning, the proportions of larval stages in the catch change constantly, and we cannot estimate the survival rate operating at a given time nor obtain any information on the effect of temperature on survival.

DIRECTION OF MIGRATION

The data on survival rate shown in figures 7 and 9 indicate that the migration pattern of the larvae radiates away from the centers of spawning and that the apparent drift is mainly in an easterly direction. Jones et al. (footnote 6) showed that

few larvae are present north and west of our area of study. Koczy, Rinkel, and Niskin (1960) investigated the current system of the region and concluded that, although the water masses are subjected to a tidal movement of 9 to 11 km. per day, the resultant movement over a full tidal cycle is slight. Also, the small resultant drift is in a westerly direction and not in the required easterly direction. Additional evidence regarding the current system has been obtained recently through the release and recovery of seabed drifters. A vector analysis of the seabed drifter returns has indicated the presence of a slow southwest drift over the shrimp grounds. The detailed results have been reported by Rehrer, Jones, and Roessler (1967). The conclusions drawn from these results are that direct dispersal to the east seems improbable and that postlarvae reaching the nursery grounds of the Everglades are carried there by currents via some indirect route.

The most likely alternative means of larval transportation is by the Gulf Stream, passing through the Florida Straits. Biologists on cruises to the Tortugas region have on many occasions reported a strong southerly current flowing through Rebecca Channel and entering the Florida Straits. Current speed was measured on one occasion at 2.6 km. per hour (1.4 knots). Because Rebecca Channel is directly southwest of the centers of spawning (stations 40.90 and 50.80), considerable numbers of larvae must be swept through the channel and into the Florida Straits.

A survey cruise in October 1964 covered an area of some 10,789 km.² between Cape Sable on the Florida mainland and the Tortugas shrimp fishing grounds (fig. 10). Additional stations were in the Florida Straits south of the Florida Keys.

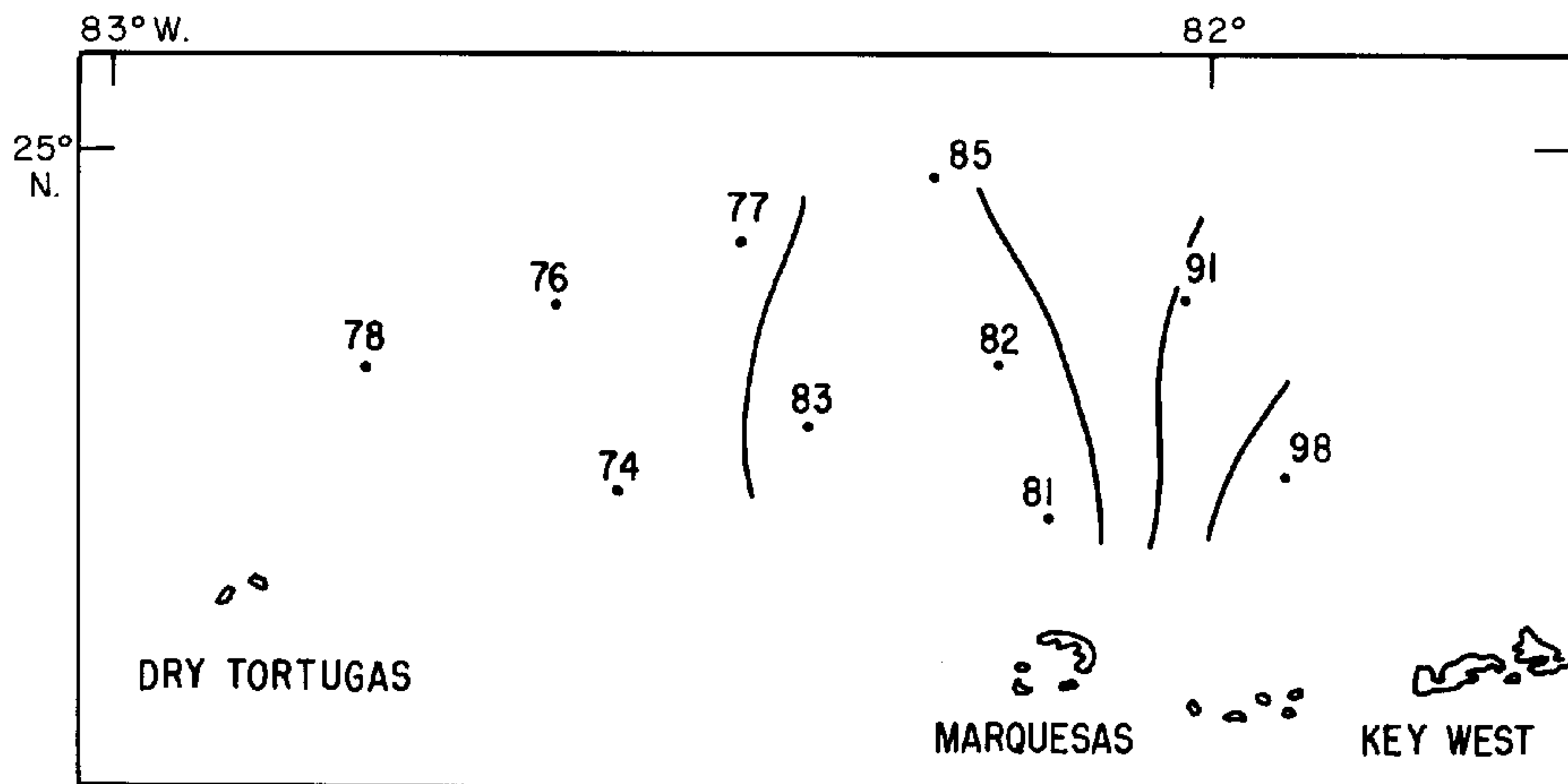


FIGURE 9.—Variations in the apparent daily survival rate between 1st protozoal and 1-spine postlarval stages of *P. duorarum* on the Tortugas Shelf, August 1962 to October 1964.

The most striking feature of figure 10 was the capture of large numbers of *P. duorarum* larvae, mainly protozoae, in the Florida Straits. These larvae were taken in the surface and midwaters of the Straits in water between 50 and 180 m. (28 and 98 fathoms) deep and at all the stations occupied. In contrast, few larvae or postlarvae were taken north of the Florida Keys.

We can, therefore, postulate that larvae are dispersed by transport out of Rebecca Channel and into the Florida Straits. The larvae would be carried eastward by the Florida Current and eddied back into the Florida Bay region by tidal currents moving through the inlets between the Florida Keys. If this transport does occur, the larvae would arrive at a point only about 37 to 56 km. from the Everglades nursery grounds, about 6 days after their exit from Rebecca Channel (calculated according to the velocity of the margins of the Florida Current given by Sverdrup, Johnson, and Fleming, 1942). The main part of the journey from the spawning grounds to the Everglades might take only a short time, leaving the bulk of the larval and postlarval life for the journey across Florida Bay, a distance of 37 to 56 km.

We have learned that postlarvae appear to react to tidal currents and ascend into the moving tide mainly during the nighttime flood tide. If this is so, movement across Florida Bay, where the

tides flow roughly north and south, might be accomplished within a week. If this migration takes place, the estimates of survival given in the preceding section must be reconsidered. We have shown that the apparent survival rate increases steadily toward the eastern sector of the sampling grounds (fig. 9). If larvae are removed from Tortugas grounds via Rebecca Channel, then their greatest loss through the channel would occur at stations nearest to the channel (viz, the western stations), and the apparently low rates of survival in this area are caused by loss of older larvae and not by movement of larvae in an easterly direction. This loss might explain the anomalous catches at station 32.70 (directly north of the Marquesas) which yield estimates of survival that are not of the same order as those calculated for station 30.58 (fig. 7a), although the stations are only 18.5 km. apart and of similar depths (14.5 and 11 m. or 8 and 6.1 fathoms, respectively). If larvae have traveled from the spawning grounds via the Florida Current, and then have been eddied back into the vicinity of station 30.58 via tidal currents in the Northwest Channel, the high proportion of older larvae and postlarvae at this station could be explained. The position of station 32.70, directly north of the Marquesas and away from any tidal channels, would preclude it from receiving older larvae.

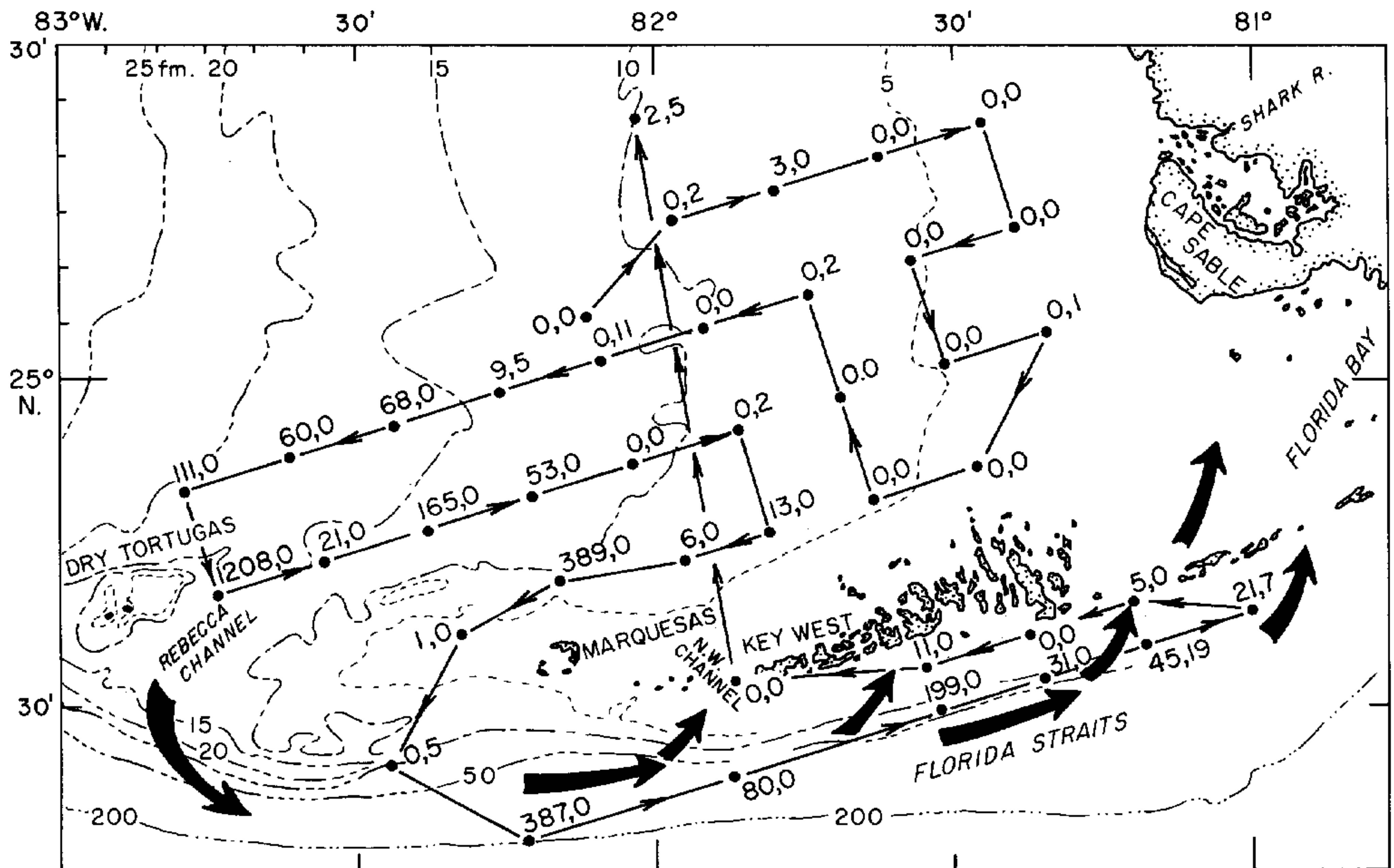


FIGURE 10.—Map of the Tortugas Shelf area showing track of Cruise 6416 (October 2 to 6, 1964) and the estimated abundance of *P. duorarum* larvae (first number) and postlarvae (second number) under 10 m.² surface area at each of the stations occupied. Probable migration route of larvae is indicated by wide dark arrows.

We, therefore, conclude that if the variations in survival at specific stations are a result of emigration in a southerly direction at the western stations and not the result of eastern stations receiving immigrants from the west, then the average rates of survival calculated from all catches may err in being slightly too low. They might be best represented by the survival at stations 40.70, 40.80, and 50.70, which are centrally located and farthest removed from the influence of Rebecca Channel and the Northwest Channel (fig. 8). Survival at these stations averages about 83 percent per day.

SUMMARY

1. The 95-percent confidence limits applicable to estimates of abundance of *P. duorarum* protozoae are such that a single estimate cannot be considered significantly different unless it is less than 29 percent or greater than 348 percent of the sample with which it is compared. This variability

is greater than that normally encountered in studies of this type, but part of the variability may be ascribed to the fact that the analysis was based upon replicate tows and not upon paired tows.

2. Gross annual production of first protozoae of *P. duorarum* within the sampling area was in the order of 870×10^{10} individuals.

3. Spawning in each year usually reached a peak during the month of the highest bottom-water temperatures. The month in which the bottom water was warmest varied from year to year, and the months of maximum spawning activity varied accordingly.

4. The center of spawning tended to move toward deeper water as the season progressed, and the last heavy spawning was in depths of more than 30 m. (16.7 fathoms). This movement may be correlated with temperature decreases in shallow water, but the movement of adult shrimp into deeper water is the factor which is most directly responsible.

5. Intramonthly variations in abundance of larvae are related to moon phase. Most spawning occurred during the waning moon (15-29 days after new moon).

6. Survival rates are nearly constant throughout the postnaupliar larval life, averaging about 80.4 percent per day. Differences in the apparent rate of survival at different sampling stations are caused by immigration and emigration of larvae between stations, by losses of larvae from stations in the path of currents which move into the Florida Straits, or by a combination of both.

7. Recoveries of seabed drifters confirm previous observations that currents in the sampling area are small (probably less than 1.8 km. per day), and that the movement of water is primarily toward the south and west. It is unlikely that larvae disperse directly toward the Everglades in the east. Available evidence indicates that dispersal may be effected primarily by the current which leaves the Tortugas area through Rebecca Channel, and enters the Florida Current in the Florida Straits. Entry into the Florida Current would result in rapid transport to the area adjacent to Florida Bay. If this migration route is the main method of dispersal and transport of larvae, then the average apparent rate of survival of 80.4 percent per day may be an underestimate, and the true rate of survival may be as high as 83 percent per day.

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LITERATURE CITED

- AHLSTROM, ELBERT H.
1954. Distribution and abundance of egg and larval populations of the Pacific sardine. [U.S.] Fish Wildl. Serv., Fish. Bull. 56: 83-140.
- ARNOLD, EDGAR L., JR.
1959. The Gulf V plankton sampler. In Galveston Biological Laboratory Fisheries Research for the year ending June 30, 1959, pp. 111-113. U.S. Fish Wildl. Serv., Circ. 62.
- BARKLEY, RICHARD A.
1964. The theoretical effectiveness of towed-net samplers as related to sampler size and to swimming speed of organisms. J. Cons. 29: 146-157.
- DOBKIN, SHELDON.
1961. Early developmental stages of pink shrimp, *Penaeus duorarum*, from Florida waters. U.S. Fish Wildl. Serv., Fish. Bull. 61: 321-349.
- ELDRED, BONNIE.
1959. A report on the shrimps (Penaeidae) collected from the Tortugas controlled area. Fla. State Bd. Conserv., Spec. Sci. Rep. 2, 6 pp.
- ELDRED, BONNIE, ROBERT M. INGLE, KENNETH D. WOODBURN, ROBERT F. HUTTON, and HAZEL JONES.
1961. Biological observations on the commercial shrimp, *Penaeus duorarum* Burkenroad, in Florida waters. Fla. State Bd. Conserv. Mar. Lab., Prof. Pap. Ser. 3, 139 pp.
- ELDRED, BONNIE, JEAN WILLIAMS, GEORGE T. MARTIN, and EDWARD A. JOYCE, JR.
1965. Seasonal distribution of penaeid larvae and postlarvae of the Tampa Bay area, Florida. Fla. State Bd. Conserv. Tech. Ser. 44, 47 pp.
- ENGLISH, T. SAUNDERS.
1964. A theoretical model for estimating the abundance of planktonic fish eggs. Cons. Perma. Int. Explor. Mer, Rapp. Proc.-Verb. Réunion. 155(31): 174-182.
- EWALD, JOSEPH J.
1965. The laboratory rearing of pink shrimp, *Penaeus duorarum* Burkenroad. Bull. Mar. Sci. 15: 436-449.
- GURNEY, ROBERT.
1942. Larvae of decapod Crustacea. Ray Soc. Publ. 129, 306 pp.
1943. The larval development of two penaeid prawns from Bermuda of the genera *Sicyonia* and *Penaeopsis*. Proc. Zool. Soc. London, ser. B, 113: 1-16.
- HELDT, JEANNE H.
1938. La reproduction chez les Crustacés Décapodes de la famille des Pénéides. Ann. Inst. Océanogr. Monaco, 18(2): 31-206.
- HUDINAGA, MOTOSAKU.
1942. Reproduction, development and rearing of *Penaeus japonicus* Bate. Jap. J. Zool. 10(2): 305-393, 46 pls.
- IVERSEN, EDWIN S.
1962. Estimating a population of shrimp by the use of catch per effort and tagging data. Bull. Mar. Sci. Gulf Carib. 12: 350-398.
- IVERSEN, EDWIN, and CLARENCE P. IDYLL.
1959. The Tortugas shrimp fishery: The fishing fleet and its method of operation. Fla. State Bd. Conserv., Tech. Ser. 29, 35 pp.
- IVERSEN, EDWIN S., and ALBERT C. JONES.
1961. Growth and migration of the Tortugas pink shrimp, *Penaeus duorarum*, and changes in the catch per unit of effort of the fishery. Fla. State Bd. Conserv., Tech. Ser. 34, 30 pp.
- IVERSEN, EDWIN S., ANDREW E. JONES, and CLARENCE P. IDYLL.
1960. Size distribution of pink shrimp, *Penaeus duorarum*, and fleet concentrations on the Tortugas fishing grounds. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 356, iv+62 pp.

- KOCZY, F. F., M. O. RINKEL, and S. J. NISKIN.
1960. The current patterns on the Tortugas shrimp grounds. Proc. Gulf Carib. Fish. Inst., 12th Annu. Sess.: 112-125.
- KORRINGA, P.
1957. Lunar periodicity. Mem. Geol. Soc. America 67: 917-934.
- McEWAN, G. F., M. W. JOHNSON, and T. R. FOLSOM.
1954. A statistical analysis of the Folsom Plankton Splitter, based on test observations. Arch. Meteorol., Geophys., Bioklimatol., Ser. A, 7: 505-527.
- MUNRO, J. L., and D. DIMITRIOU.
1967. Counts of larval penaeid shrimp and oceanographic data from the Tortugas Shelf, Florida, 1962-64. U.S. Fish Wildl. Serv., Data Rep. 16, 40 pp. on 1 microfiche.
- PEARSON, JOHN C.
1939. The early life histories of some American Penaeidae, chiefly the commercial shrimp *Penaeus setiferus* (Linn.). U.S. Bur. Fish., Bull. 49: 1-73.
- REHRER, R., A. C. JONES, and M. A. ROESSLER.
1967. Bottom water drift on the Tortugas grounds. Bull. Mar. Sci. 17: 562-575.
- SAVILLE, ALAN.
1964. Estimation of the abundance of a fish stock from egg and larval surveys. Cons. Perma. Int. Explor. Mer, Rapp. Proc.-Verb. Réunion. 155(29): 164-170.
- SETTE, OSCAR E., and ELBERT H. AHLSTROM.
1948. Estimations of abundance of the eggs of the Pacific pilchard (*Sardinops caerulea*) off southern California during 1940 and 1941. J. Mar. Res. 7: 511-542.
- SILLIMAN, RALPH P.
1946. A study of variability in plankton tow-net catches of Pacific pilchard (*Sardinops caerulea*) eggs. J. Mar. Res. 6: 74-83.
- STRASBURG, DONALD W.
1960. Estimates of larval tuna abundance in the Central Pacific. U.S. Fish Wildl. Serv., Fish. Bull. 60: 231-255.
- SVERDRUP, H. U., MARTIN W. JOHNSON, and RICHARD H. FLEMING.
1942. The oceans, their physics, chemistry and general biology. Prentice-Hall, Inc., New York, 1087 pp.
- TABB, DURBIN C., DAVID L. DUBROW, and ANDREW E. JONES.
1962. Studies on the biology of the pink shrimp, *Penaeus duorarum* Burkenroad, in Everglades National Park, Florida. Fla. State Bd. Conserv., Tech. Ser. 37, 32 pp.
- TAFT, BRUCE A.
1960. A statistical study of the estimation of abundance of sardine (*Sardinops caerulea*) eggs. Limnol. Oceanogr. 5: 245-264.
- U.S. FISH AND WILDLIFE SERVICE.
1964. Gulf Coast shrimp data—1963. Its Curr. Fish. Statist. 3515, 53 pp.
- WINSOR, C. P., and G. L. CLARKE.
1940. A statistical study of variation in the catch of plankton nets. J. Mar. Res. 3: 1-34.